

events (for recent reviews see Walliser, 1996; Hallam

Timing of extinction

Turning to the temporal aspects of extinction, high-resolution dating has dramatically altered estimates of extinction duration and rates throughout the Phanerozoic (see methods in Harries, 2003; Gradstein et al., 2004; Erwin, 2006a). For example, detailed examina-

which postulate either a single cause or a combination of every possible cause for each event (Jablonski, 1980; MacLeod, 1998). It is entirely likely that multiple causes are responsible for these events and only careful hypothesis testing, coupled with fine-scale dating, geochemical tools, and selectivity analyses (see for example Knoll et al., 2007), will help us to differentiate the importance and timing of different mechanisms. Although the stated goal of many selectivity analyses is to identify possible causal mechanisms, few studies have proven successful, in part due to the dearth of explicit hypotheses generated to differentiate among causes, no doubt coupled with few opportunities to integrate vital paleoenvironmental and paleoclimate data.

Recovery

Turning to recovery intervals [i.e., post-extinction intervals characterized by rapid rebound of diversity (Erwin, 2001)], we are still in need of the most basic data when it comes to recoveries, including: (1) rates, (2) durations (for a start see table 1 in Erwin, 1998), and (3) the effects of a range of biases on these patterns. Detailed descriptions of these intervals have shed some light on which taxa are participating in the repopulation and to what extent (Harries et al., 1996). Repeated mentions of bloom and/or opportunistic taxa emphasize the need for a quantitative and/or phylogenetic approach to identifying the key players in recovery, from “disaster forms” (i.e., defined as simple, cosmopolitan, opportunistic generalists: Schubert and Bottjer, 1995) to examples of “dead clade walking” (e.g., defined as survivors that do not participate in the post-extinction diversification: Jablonski, 2002). We need more outcrop-scale studies, combined with regional analyses and phylogenetic tracking (e.g., Rode and Lieberman, 2005; McGowan and Smith, 2007) across both extinction and recovery intervals, to properly differentiate survivors from taxa originating in the post-extinction melee.

PRESERVATION, SAMPLING, AND OTHER FACTORS

In the past decade, our understanding of the extent to which factors such as preservation and sampling affect global estimates of extinction and diversity in the

fossil record has grown by leaps and bounds. To generalize, better preservation and greater sampling yield greater sample diversity, which becomes a problem when we try to reconstruct large scale diversity and extinction patterns in the fossil record. To consider the best- and worst-case scenarios, perfect preservation and sampling produce 100% accurate stratigraphic ranges and therefore 100% accurate extinction rates. In contrast, extremely poor preservation and sampling convert all taxa into singletons (i.e., taxa that are restricted to a single time interval) and extinction rates become meaningless. In reality, preservation and sampling lie somewhere between these two scenarios, but they illustrate the importance of estimating preservation rate and standardizing sampling concurrently with extinction rate (Foote and Raup, 1996; Foote, 1997). Peters and Ausich (2008) provide a useful framework for categorizing the numerous factors that distort the macroevolutionary record. They subdivide them into intrinsic (i.e., those that are intrinsic to the scientific process of accumulating knowledge, including incomplete sampling and taxonomic errors) versus extrinsic ones (i.e., those that are inherent to the geological record itself, such as rock availability, sequence architecture, and taphonomic factors).

To consider intrinsic factors first, variable sampling (i.e., differences in sample sizes across time intervals) can massively distort estimates of diversity (see Alroy et al., 2001; Bush et al., 2004, among many others) and must be taken into account before any attempt is made to quantify extinction. Sample standardization is often accomplished by applying boundary-crosser metrics (Bambach, 1999; Foote, 2000), removing singletons (Sepkoski, 1996; Foote, 2000), or perhaps more effectively via resampling routines (Alroy et al., 2001) such as rarefaction. It should be noted that sample standardization, which adjusts for variable as opposed to incomplete sampling, does not eliminate the problems associated with the Signor-Lipps effect (see below).

The impact of another intrinsic factor—taxonomic standardization—on global compilations of diversity has been debated for years (Smith and Patterson, 1988; Sepkoski and Kendrick, 1993; Wagner, 1995a;

cused on three molluscan case studies throughout the Phanerozoic and found that taxonomic standardization elevated extinction rates in at least one of their case studies (Paleozoic gastropods). They argued that an overabundance of polyphyletic taxa, coupled with high species richness in paraphyletic taxa, acts to artificially diminish the magnitude of extinction events (see also Uhen, 1996). In contrast, Ausich and Peters (2005) found that substantial revision of crinoid taxonomy yielded significantly lower extinction rates in the Late Ordovician. These results highlight the influence of phylogenetic topology on extinction rates, and emphasize the importance of explicitly controlling for taxonomic bias.

Turning to extrinsic factors, several studies have revealed that the available rock record is strongly correlated with diversity curve shape; decreases in outcrop availability artificially inflate estimates of extinction intensity (Raup, 1972; Peters and Foote, 2001; Smith, 2001; Peters and Foote, 2002; Crampton et al., 2003; Foote, 2003). A number of other extrinsic factors that potentially affect the “completeness” of the record (and hence extinction rates) have been identified, including secular patterns in sequence architecture (Holland, 1995; Smith, 2001; Holland, 2003) and taphonomic and diagenetic factors (Cherns and Wright, 2000; Kidwell and Holland, 2002; Wright et al., 2003; Kowalewski et al., 2006); however, few studies have explicitly quantified the influence of these factors (for example see Bush and Bambach, 2004).

Another extrinsic artifact, “Pull of the Recent,” occurs when increased sampling of the Recent biota extends stratigraphic ranges of fossil taxa, artificially decreasing estimates of extinction towards the present day. Recent analysis of extant and Plio-Pleistocene bivalve subgenera revealed that only 5% of Cenozoic diversity could be explained by “Pull of the Recent” (Jablonski et al., 2003). This result suggests that this particular artifact may not be as much of a problem as originally thought, although analysis of other clades is certainly warranted (see also Foote, 2000).

One useful approach to measuring a combination of extrinsic factors, such the completeness of the fossil record (among many, for review see Foote, 2001), takes advantage of the expected inverse relationship between the number of singletons and preservation quality, and only requires data on the first and last occurrences of taxa (Foote and Raup, 1996; Foote, 1997). This technique, FreqRat (Foote and Raup, 1996), es-

timates preservation probability per unit time interval given the frequency of taxa with stratigraphic ranges of 1 (i.e., singletons), 2, and 3 intervals. This, in turn,

The history of life has a sample size of one and as a result, paleontology is generally considered a historical, as opposed to experimental, science. This view, along with the seemingly overwhelming number of differences among extinctions, has limited our ability to systematically identify and synthesize patterns across the Phanerozoic. Although the analogy is far from perfect, viewing extinctions as repeated natural experiments in the history of life would allow us to identify common features characterizing and processes underlying these events. The analogy can be extended further by considering several of the aspects of extinction that are already well-constrained— such as magnitude, duration, tectonic configuration, and climate— as controls for these natural experiments. For example, to target questions concerning the evolutionary effects of extinction according to magnitude, one could select 3-4 extinctions along a gradient of magnitude, all associated with broadly similar causal mechanisms, such as climate change. A plethora of new and newly refined tools, including CONOP-9 [i.e., Constrained Optimization (Kemple et al., 1995)], biomarkers, and GIS [i.e., Geographic Information Systems (Graham et al., 1996; Rode and Lieberman, 2004; Stigall and Lieberman, 2006)], allow us to take a much more holistic approach to these natural experiments. Testing of cause and effect hypotheses requires interdisciplinary, integrated methods, merging disparate fi

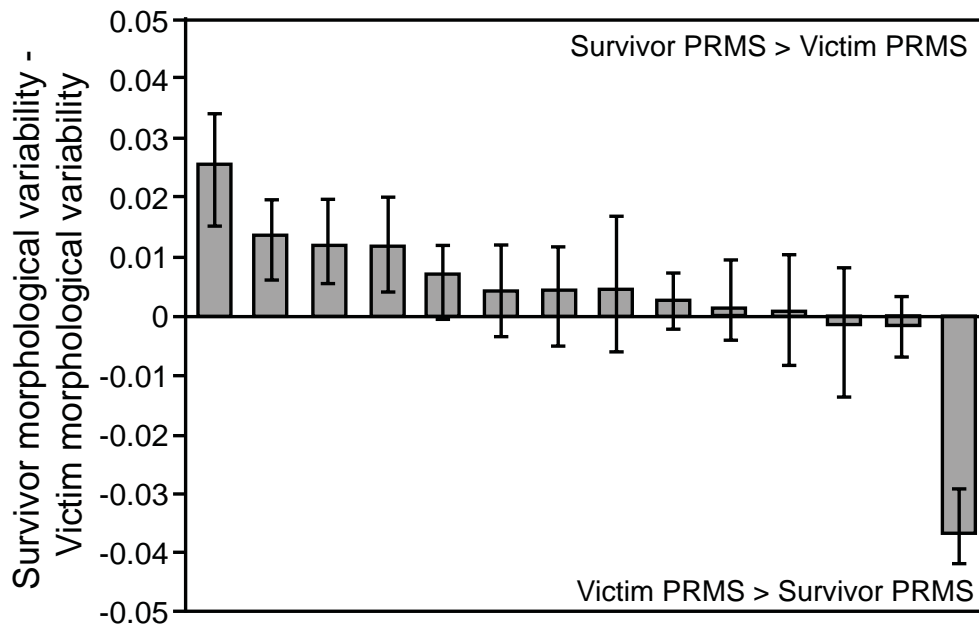
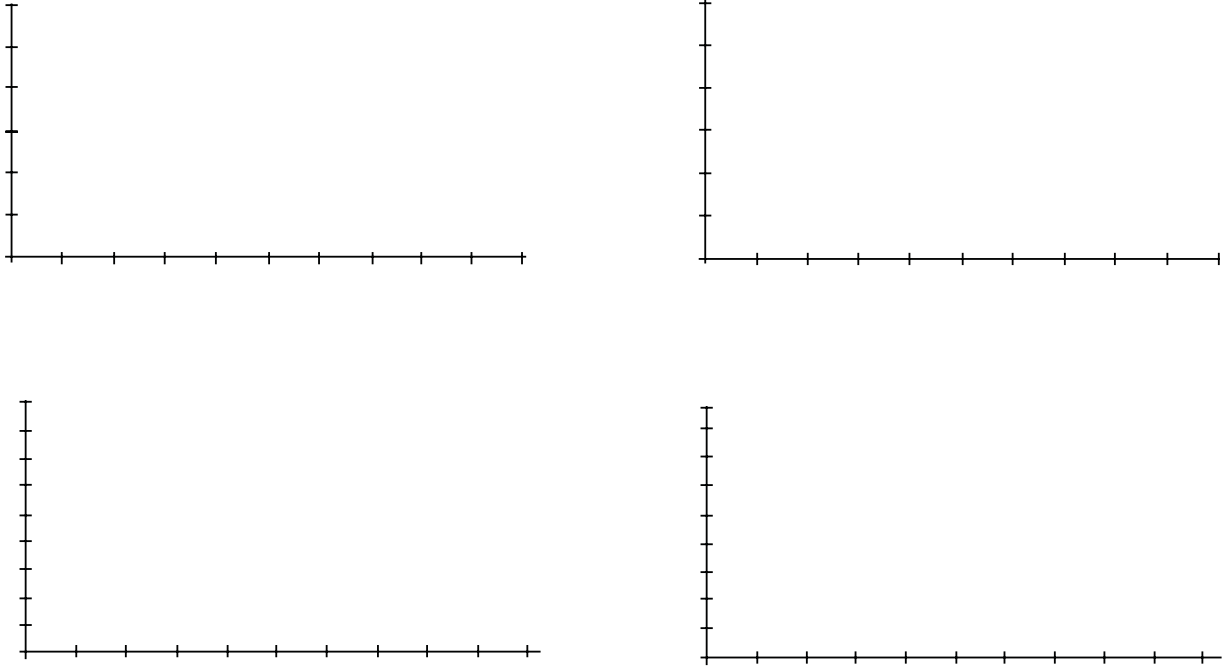


Figure 2—Effects of morphological variability on survivorship in veneroid bivalves from the Plio-Pleistocene extinction in Florida. Each bar represents a closely related pair of species, one of which is a victim and the other is a survivor. Pairs that plot above the x-axis have survivors with more morphological variability than victims. Pairs that plot below the x-axis show the opposite. Error bars represent 95% confidence intervals obtained via bootstrap resampling. In general, species with more morphological variability are more likely to survive the extinction (modified from Kolbe et al., 2006)

the link between morphological variation and extinction, two recent studies suggest that variation may also influence pathways and rates of diversification. Hunt (2007) empirically examined the interactions among morphological variation and evolutionary divergence in the ostracode genus *Poseidonamicus* and found that evolutionary changes tended to occur in directions of high phenotypic variation within the genus. Similarly, Webster (2007) determined that the incidence of polymorphic characters (i.e., characters which span two or more states of variation in a given taxon) was higher in stratigraphically older and/or phylogenetically basal species of Cambrian trilobites. The possible link between trait variation and extinction is intriguing and leads to a number of hypotheses that can be tested at a variety of taxonomic levels, including the possibility that taxa with more variability should be more likely to survive and more likely to recover more quickly. These hypotheses require testing across multiple clades and events, especially in light of possible implications for the conservation and management of modern biodiversity.

The traditional approach to quantifying selectivity, independently testing a handful of traits in a single clade across a single event, is slowly giving way to much more robust multivariate analyses that take non-linear covariation among traits explicitly into account. Biological traits, regardless of whether they are life history, ecological, or morphological in nature, are inexorably linked to one another, and these linkages can make it difficult, if not impossible, to determine which traits are being selected for and which traits are simply along for the ride. Multifactorial approaches (e.g., Harnik, 2007; Payne and Finnegan, 2007), such as linear and logistic regression, path analysis, and structural equation modeling (Shipley, 2000), make it possible to identify which traits are most directly related to survivorship. In an analysis of Eocene bivalve species from the U.S. Gulf Coastal Plain, Harnik (2007) reported that, although both geographic range and body size were tied to extinction probability (and to each other), the former exerted a much stronger effect than the latter (see Jablonski, 2008b for the K/T). Similarly, Payne and Finnegan (2007) used binary lo-



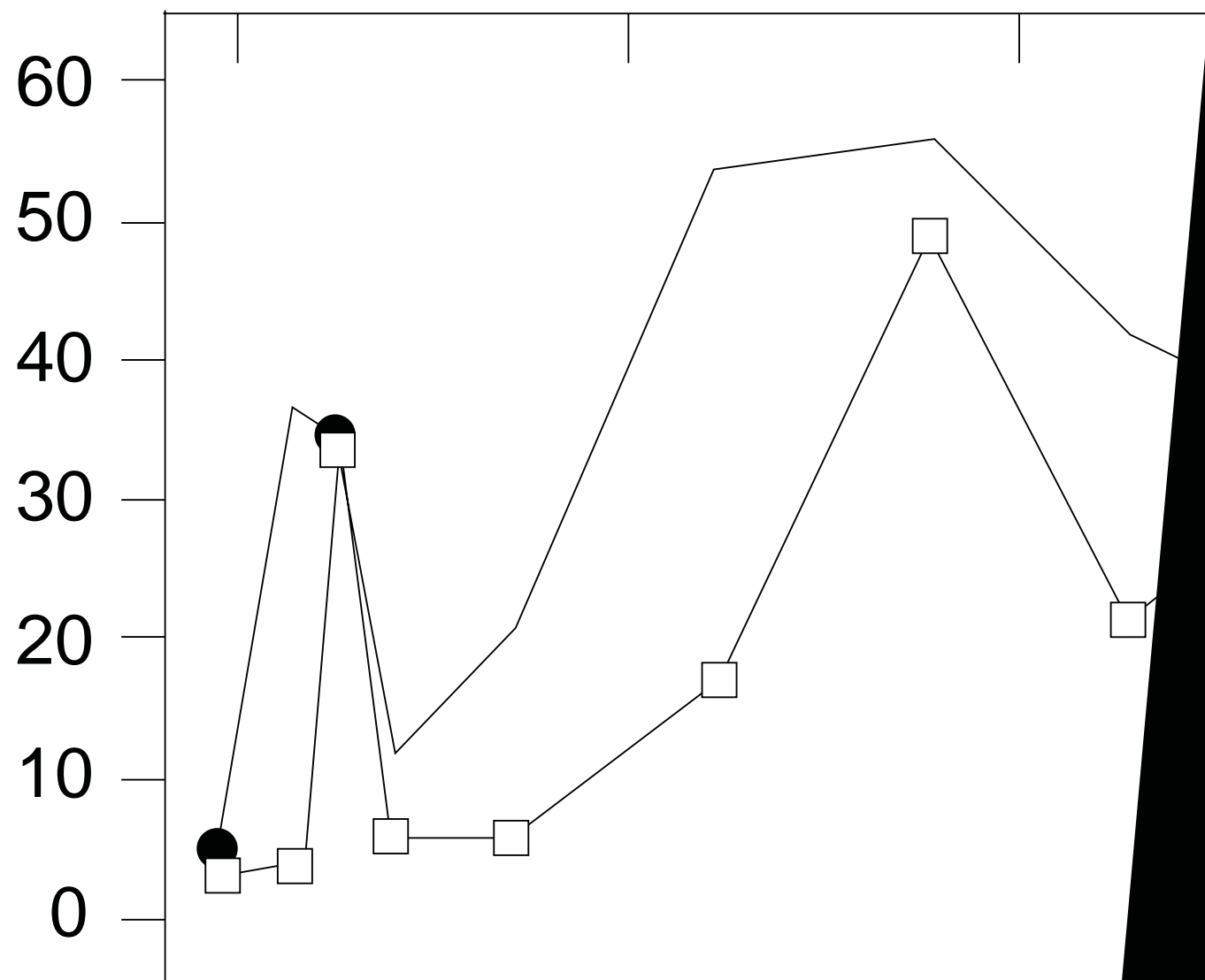
gistic regression to assess extinction selectivity during background intervals in Phanerozoic marine invertebrate genera and determined that geographic range remained a significant predictor of survivorship, even after the effects of species richness and occupancy had been removed. Such approaches are long overdue and may even help us to differentiate cause from correlation when it comes to traits that promote extinction in modern taxa.

Studies of minor and background extinction have taken a back seat to mass extinction for decades. We know far too little about how selectivity varies across extinctions of different magnitudes and durations (Johnson et al., 1995; Smith and Roy, 2006). Returning to the analogy of natural experiments, comparisons could preferentially target extinctions with similar causes, magnitudes, or durations, in an effort to reveal differences in selectivity relative to other aspects of the events. A comparison of selectivity according to body size in veneroid bivalves across the K/T, end of the middle Eocene (mid-E), and end Eocene

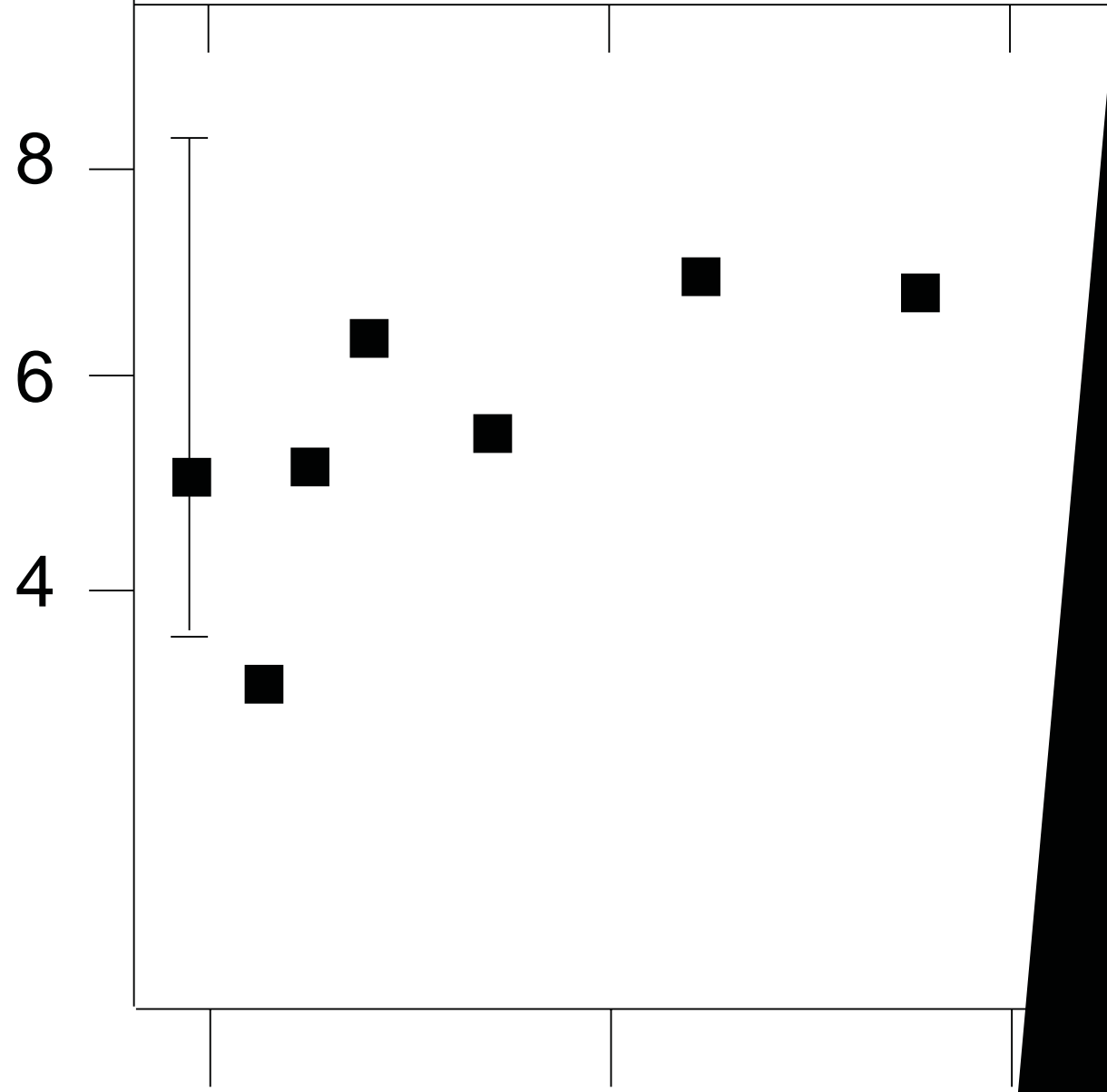
(E/O) events in North America and Europe suggested that the lower magnitude, but longer duration event was associated with statistically stronger selectivity (Lockwood, 2005). Although neither extinction was size selective, the K/T recovery was biased towards smaller veneroids, while the mid-E and E/O recoveries were biased towards larger veneroids (Fig. 3). This result raises the interesting possibility that longer term “press” extinctions, in which the extinction pressure is prolonged, may exhibit stronger selectivity and therefore exert stronger influence on evolutionary trends than short-term “pulse” extinctions (Erwin, 1996b). This interpretation is complicated, in this case, by the extremely different causal mechanisms for these events (i.e., bolide impact for the K/T and climate change for the Eocene events). Payne and Finnegan’s (2007) comparison of selectivity during background and mass extinction intervals for Phanerozoic marine invertebrate genera documented a weak, but intriguing, inverse relationship between extinction magnitude and geographic range selectivity. Selectivity for broad

the different starting points for each diversification in ecospace—an empty ecospace in the early Paleozoic versus a sparsely occupied ecospace in the Mesozoic.

Number of genera



Morphological variance



pects of extinction, including the relative importance of extinction, origination, and migration, during both extinction and recovery intervals, have received relatively little attention thus far.

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